
Review of the National Marine Mammal Laboratories Steller Sea Lion Telemetry Program

Mark A. Hindell

Antarctic Wildlife Research Unit
School of Zoology
University of Tasmania

EXECUTIVE SUMMARY

This is a review of the National Marine Mammal Laboratory's (NMML) Steller sea lion telemetry program. The scope of the review was to focus on four important aspects of the program: The appropriateness of the programming and deployment strategies; the appropriateness of the methods used to retrieve and manage telemetry data obtained from Service Argos; the appropriateness of the stage-based filtering algorithm used by the NMML; and the determination of whether potential biases and appropriate measures of statistical uncertainty have been included.

The NMML telemetry program has been a driving force in the development of satellite telemetry in the past 20 years, and many of the innovations made by this team have been of considerable benefit to the discipline in general. The end point of their research efforts is to provide the best possible information to aid in the conservation and management of this endangered species, and the team is well placed to continue as a leader in the field. After the meeting held with NMML scientists in Seattle June 2-3, 2004, I found that:

1. With respect to Scope Item i (SDR programming and deployment strategies), I felt that the team has done an excellent job developing the appropriate sampling and transmission protocols to be used on the SDRs. However, the devices used in the past have in-built limitations, largely due to the use of "binned" summaries of behavioural data. To date these limitations have not been a problem and the information collected has been sufficient to answer most of the important questions (such as identification of critical habitat). The team will however need to obtain better data on foraging behaviour to address emerging questions of habitat use, and this will require the use of better on-board summaries and data transmission. The deployment strategies used so far have to large extent been driven by the requirement to study juveniles. Access to this age group has been difficult, but adopting the SCUBA capture technique and developing the new "raft traps" has greatly increased the teams ability to conduct properly stratified designs. Another difficulty is the remote location of the seal's haul-outs, particularly in the Gulf of Alaska. However the team, in conjunction with the Alaska Department of Fish and Game, has managed to sample a large number of regions. There are now sufficient data to assess the appropriateness of the sample sizes in each region and to attempt some state-based "population" level spatial usage analyses.
2. I found that the team is very advanced regarding Scope Item ii (data retrieval and database). The system developed for retrieval, storage, linkage to other data sources and access to analytical packages was excellent, and is likely to be of use to others working in similar fields. However, there was a clear need to coordinate all of the other sources of telemetry data for this species. The NNML database is an obvious repository for these data. Management of this species can only be better informed if complete information is used to address the key issues. While issues of intellectual property may hamper this, I feel every attempt should be made to improve data sharing between research labs.
3. The stage-based filter developed by NMML (Scope Item iii) was a sophisticated version of other "destructive" filters that are widely used in the marine mammal community. The filter provides the 4 best quality locations that correspond to the 6-hourly "binned" dive data summaries transmitted by the SDRs. This removes much of the potential biases caused by behaviour of the seals and intermittent satellite coverage, but it has the problem of also throwing away the majority of the data. Adopting the newly emerging "path analysis" models of animal movements will enable maximum use of the complete data set, while also incorporating uncertainty information.
4. The team has recognised most of the potential biases in the data (Scope Item iv), and has worked to minimise them. Adopting the emerging SDR technology and data analysis approaches outlined above will further reduce biases and improve the quality of information available.

Overall Recommendations

I have made several recommendations throughout the report, which I hope will be of use to the team. These can be summarised as follows.

1. There is not the required level of mathematical skills in the team to take advantage of emerging analytical tools, such as path analysis and state-based models of spatial usage patterns. The appointment of a Seattle based mathematician to work on these issues will ensure the NMML lab stays at the forefront of marine mammal telemetry.
2. There needs to be high level of coordination and collaboration between groups collecting telemetry data on Steller sea lions. This could be achieved through central storage of data and regular workshops.
3. Greater levels of collaboration and sharing of expertise with other research groups need to be encouraged, and most importantly, funded.
4. I felt that the review by a panel of independent experts was a very constructive exercise. Similar reviews of other aspects of the Steller sea lion program would benefit the program and contribute to the overall aim of enhancing the management of this species.

Introduction

The Gulf of Alaska (GoA) populations of the Steller Sea Lion (*Eumetopias jubatus*) have declined dramatically over the last 30-40 years. The cause, or causes, of this decline are still unknown, but attempts to identify the major causal factors have led to a large body of research into many aspects of Steller Sea Lion (SSL) biology. Several of the most important questions concern the at-sea movements of the seals. Prior to the development of telemetry systems appropriate to SSL, little was known about movements between colonies, haul-out patterns, foraging areas or foraging behaviour for this species. Another important contribution of the at-sea data concerned the potential indirect interactions with the GoA commercial fishing fleet, and the consequent requirement to identify management zones. In recent years much of the focus of this research has been on juveniles, as demographic studies have revealed that poor survival in this component of the population is a key factor driving the population declines.

The National Marine Mammal Fisheries Laboratory (NMML) have been working on quantifying the at-sea movements of SSL since the 1980's and has been a pioneer in the development of satellite telemetry techniques. The most commonly used and versatile devices are those that record behavioural data (such as dive depths, dive durations and haul-outs) and transmit this information to polar orbiting satellites, which also calculate the position of the seal. These devices are known as Satellite-linked Data Recorders (SDRs). At present NMML is one of 5 research groups studying aspects of the movements of SSL, and with more than 140 successful deployments of satellite transmitters, it has amassed the largest data set. The SSL team at NMML also developed a database to manage these, and other, data, established programming protocols for the SDRs, and along with a suite of data analysis tools for "filtering" (removal of incorrect locations) and interpreting the behavioural and location data. The team's efforts have, amongst other things, been used to identify areas of critical habitat for the GoA SSL.

The specific scope of this review was to consider:

- (i) The appropriateness of the programming and deployment strategy of SDRs on juvenile Steller sea lions
- (ii) The appropriateness of the methods used to retrieve and manage telemetry data obtained from Service Argos
- (iii) Appropriateness of the stage-based filtering algorithm used by the NMML to detect haul-out periods and to evaluate the geometry and velocity of movements at sea
- (iv) Determination of whether potential biases have been adequately identified, and whether appropriate measures of statistical uncertainty have been included

The panel of independent experts (Professor Ian Boyd, Sea Mammal Research Unit (SMRU), Mr Bernie McConnell, SMRU, and Associate Professor Mark Hindell, Antarctic Wildlife Research Unit) met the National Marine Fisheries Service SSL research team at the National Marine Mammal Laboratory, Seattle, on 2 - 3 June 2004. The panel heard several presentations from the team tailored to address the scope items outlined above. Individuals from the panel asked questions throughout, and the resulting discussions have been used as the basis of this report.

The report will address each of the scope items in turn, outlining my opinions and, where appropriate, specific recommendations for the SSL team to consider in its future research. From the outset, it is important to recognise that there was considerable overlap between the scope items, particularly when addressing potential biases, and this is at times reflected in what I have written. As far as possible, however, I have tried to adhere to the underlying four-point structure.

i. The appropriateness of the programming and deployment strategy of SDRs on juvenile Steller sea lions

I found that that the programming and deployment of instruments has been an evolutionary process, which has changed in response to increasing biological knowledge and technological and logistic capacity. Part of the innovation exhibited by the SSL team has been to ensure that the most up-to-date technologies are being used (but see my comments on the nature of the on-board data collection and its subsequent summary and transmission below).

Access to animals.

An on-going challenge to the team has been its ability to capture animals for the deployments of telemetry units, and the team has done well to develop and modify approaches to meet this challenge. Initially, the team used disruptive hoop-netting techniques at the haul-outs, which provided little control over the characteristics of the animals captured, and perhaps even biased samples towards the “sick and the lame”. The team then moved to the SCUBA lasso techniques, which enabled it to capture the important juvenile seals for the first time. Although a considerable advance, this technique still has several disadvantages such as inter-individual (and perhaps even sex-biased) catchability and lack of access to other age classes, such as adult males. I found the recent development of “raft traps” to be very exciting, as this will provide access to animals of different age and sex classes and has the potential to allow the stratification of sampling to offset potential biases from the over-sampling of particular age and sex classes. This will revolutionise all areas of SSL research, not just the telemetry components.

Programming and on-board sampling protocols.

To date, the majority of SDRs used in the NMML SSL program have been provided by Wildlife Computers. Although these units have performed remarkably well, the nature of the questions now being asked by the team regarding finer-scale foraging behaviour cannot be met with the present on-board sampling and data summary protocols of these units. The placement of behavioural data into pre-programmed “bins” transmitted as 6-hour summaries is particularly limiting. Although this form of data collection was initially designed to overcome the constraints of low transmission baud rates from the SDRs to the satellite, new systems of data compression and on-board analysis (such as those used in the SMRU SDRs) have been developed which provide much more detailed data on individual dives. The SSL team has continued to use the old data collection routines in order to maintain a consistent data collection protocol, the Steller sea lion research. However, I was pleased to note that the SLL team are now using alternative SDRs (from (SMRU) with more up-to-date and comprehensive data summary protocols to address specific questions of fine-scale foraging behaviour.

Given the constraints inherent in the SDRs, the SSL team has done well in maximising the location and behavioural data that they have received. The team has changed the way in which they program the SDRs over the years partly in response to changing research priorities and partly in response to improved understanding of the seal’s biology. There have been three important refinements to the programming.

1. The units are now duty cycled to transmit only 4 hours in every 6, and these transmissions are timed to correspond with satellite passes.
2. The units are also programmed to transmit more frequently than before. These two modifications have resulted in a substantial increase in the mean number of “hits” received by the satellites each day over the last 10 years. I recognise that some of this increase is due to improvements in Service ARGOS, but the changes made in the transmission protocols were most important.
3. The team has also increased the priority of the time-line data transmitted by the SDRs. Timeline data is a 20 minute summary of whether the SDR is dry or wet, and is important to the team when interpreting and filtering the data (see next section). The frequency of time-line transmissions (and therefore the likelihood of the data being received by a

satellite) is one parameter that can be modified by the user, and the team has modified its protocols to maximise the reception of these data.

Deployment strategies

In addition to using the most appropriate sampling protocols on the SDRs, the team has also had to develop the most appropriate deployment strategies to answer their key questions. The important issues here relate to how best to stratify the samples in terms of location, time and demographic characteristics of the seals (age, sex reproductive status etc). NMML has so far distributed its tagging effort among 32 sites from Washington State along the Aleutian chain to Russia, although it is acknowledged that the outer Aleutian Islands and the Russian sector are least well sampled. Given the occasional long-distance movements of sea lions between sites, and the resulting interchange of animals between sites, it is likely that the spatial distribution of population sampling give a reasonably accurate, and unbiased, impression of foraging behaviour. The differences in behaviour that have been observed between regions appear to be small. With larger sample sizes it should be possible to include region as a covariate in the estimation of uncertainty around foraging ranges.

It is also important for the team to use its existing data to assess the degree to which the populations spatial use patterns have been captured by their current sample sizes. This is in a sense a power analysis, and it will provide an indication of the number of animals that need to be tracked to obtain a complete picture of the regions that are used while at sea. A full description of one approach to this can be found in Hindell et al., 2003. This study used a large sample of individual tracks of adult female elephant seals from Macquarie Island to determine the minimum number of seals (tracks) required to capture all of the spatial information contained in the data (this is also helpful for determining sample sizes for future studies).

I believe that the SSL team has done a good job in their deployment of the units in the GoA to date, acknowledging the difficulties inherent in access the remote sea lion colonies. They have adopted a strategy of concentrating on 2-3 major regions that they can access and that are also close to areas that are used the fishing fleet. The team ultimately aims to use the data collected from these colonies to estimate spatial usage patterns at other colonies, based on statistical analysis of geographic and oceanographic covariates. It has already started this process and a draft manuscript was provided, indicating that there were, admittedly weak, correlations between SSL spatial usage and some physical oceanographic variables.

This is a promising approach, but I felt that it needed to move away from providing information on a sample of individuals to providing quantitative estimates of the entire population. This can be done using a state-space approach and including estimates of uncertainty into the data analysis. State-space models offer the possibility of assigning to each habitat feature the degree to which it helps to explain the foraging distribution of the seals.

There have been two recent studies illustrating how this might be done. Hindell et al 2003, used a bootstrapping procedure, to estimate average usage rates (with associated errors) for regions of the southern ocean, for the entire Macquarie Island population of adult females. An alternative approach is that of Matthiopoulos et al., 2004, who used sophisticated Bayesian models incorporating data on grey seal colony size and an underlying location likelihood distribution (see Matthiopoulos, 2003a; Matthiopoulos, 2003b) to provide usage maps for the entire UK.

Recommendations:

A major problem facing all SSL biologists is that this is very difficult species to study, particularly concerning access to animals. These difficulties require researchers to adopt a range of innovative approaches to animal capture, as well as following their movements at sea. As outlined in the introduction, the NMML SSL team has played a key role in the development and use of SDRs, which has benefited the entire marine mammal research community as well as providing data fundamental to understanding the decline and managing the species in the

presence of the GoA fishing fleet. From our discussions, it was clear the team is continuing to be innovative, particularly with respect to the programming and deployment of satellite tags. I feel that NMML should maintain its leadership in the field of the development of new basic technologies.

- I recommend that investments in these innovations in capture methods should be continued.
- The SSL team should move away from the “binned” data approach to data summary and transmission, and encourage manufacturers to improve their SDRs accordingly.
- The SSL team should consider conducting power analyses to assess the level of individual variation in spatial use and the representativeness of the sample sizes at the key colonies.
- NMML should combine the current data about foraging patterns derived from satellite telemetry with data about distribution and abundance at haul-outs to derive an estimated distribution for the population as a whole, by developing state-space approaches to the modelling of sea lion distributions.

ii. The appropriateness of the methods used to retrieve and manage telemetry data obtained from Service Argos

The panel examined the database developed by the SSL team. I thought that the database and its associated procedures of retrieval of data from ARGOS, quality control and back up were of a very high standard. Likewise, links to other data sources, such as satellite remote sensed sea surface temperatures and altimetry, were world-class.

One aspect of the database that I particularly liked was that the structure was sufficiently flexible to deal with behavioural and location data from a range of sources, including:

1. Conventional time-depth recorders (TDR)
2. Binned data commonly transmitted by the SDRs used by the SSL team
3. Data from location only platform transmitter terminals (PTT).

The database also included useful meta-data such as scanned data collection forms, and subsequent use of data (including which data were used in specific publications and documents). I can see considerable scope for this database to be used by other groups collecting similar types of data.

The SSL team is currently moving the database from Access to SQL Server. This is necessary to improve the capacity to interface the database with web-based tools. The current database system allows the selective release of data to stakeholders and the public. I also note that the team is developing an improved, broader data access policy, which seems to be a sensible and pro-active initiative.

The links between the database and other analysis programmes such as Arcmap were excellent. I know from my own work in this area how problematic this can be. The panel was given a demonstration of how the oceanographic data can be imported quickly into Arcmap, together with data from the SSL database, to examine relationships between movement patterns and environmental factors. The team have obviously considered the various environmental databases available (e.g. MODUS vs. Pathfinder for Sea Surface Temperature) and made appropriate choices based on the nature of their data and the questions being asked of it. There would seem to be considerable potential for the SSL team to embrace emerging GRID technologies to improve access to synoptic environmental data.

One shortcoming common to all studies using satellite-remotely sensed oceanographic data is the low spatial resolution (relative to the resolution of the seal locations) and the relatively poor coverage of the inshore regions. Given that the seals spend such a high proportion of their time

inshore, this later problem has hampered the analysis of factors influencing the spatial usage patterns described in the preceding section. The SSL team recognises this problem, and I agree with the team that there is no simple solution. Additional oceanographic data could be collected by platforms of opportunity, such as NMFS vessels, but this would, at best, provide sporadic coverage. An alternative approach is to use the seals themselves to collect sea temperature (and even salinity data) via data loggers. As the seals are very difficult to re-capture, these data would need to be relayed via satellite. I was pleased to note that the SSL team has begun to do this using new SDRs recently developed at SMRU.

My largest concern raised in the discussion of this scope item was not about the NMML database, but rather the lack of integration with other telemetry studies on SSL. The data being used by NMML does not constitute all of the telemetric Steller sea lions as there are at least four other research groups collecting data of this kind. Due to their close partnership with Alaska Department of Fish and Game (ADF&G) some data sharing takes place but there are other groups collecting Steller sea lion data and any assessments of foraging behaviour ought to include these data sets. Although this is a situation beyond the control of NMML it is unfortunate that all available data cannot be used for certain key tasks. NMML appears to have access to all the data for Steller sea lions in regions that are associated with the imposition of conservation measures (i.e. the GoA); however, there would be much to be gained from carrying out range-wide analyses of the data. Comparative studies of ranging and foraging behaviour in declining and stable populations are one obvious question that may provide important insights into the cause of the decline.

Recommendations:

- Extend the use of CTD tags to obtain physical oceanography data to help interpret, and extrapolate, spatial usage patterns.
- NMML should be encouraged to move towards a system providing broad access to data as quickly as possible.
- Efforts should be made to secure the SDR data collected from all SSL research groups within this single central database (after the establishment of access agreements with the various stakeholders). This could then be regarded as a community database.
- Regular (biennial?) workshops of researchers working on SSL telemetry, with a view to address key questions requiring comparative data.

iii. Appropriateness of the stage-based filtering algorithm used by the NMML to detect haul-out periods and to evaluate the geometry and velocity of movements at sea

The panel went into this scope item in some detail, as we felt that maximising the data obtained from SDRs was central to making informed management decisions. These require quantifying the foraging ranges of SSLs at spatial scales that are small in relation to the level of noise the location data. This is because the seals often make short trips close to shore (< 10 km and < 6 hours), and the level of accuracy associated with ARGOS locations (at least the poorer quality ones) can be of similar magnitude, making it difficult to, first determine if the seal is actually at sea (or still hauled out), and second, to determine its most likely position while at sea.

NMML Filter

The SSL team has developed a stage-based filter to deal with these problems. The filter progressively takes into account the quality of a particular location, the behaviour of the seal at the time of the location (i.e. does the diving data or the time line data indicate that the seal is on land or at sea?), the maximum likely rate of travel between locations, and finally reducing the data down to the single highest quality location that corresponds to each 6 hour summary of dive behaviour. Thus the filter progressively eliminates locations with low plausibility. Without appropriate filtering, the simple method of plotting (and counting) locations may well produce biases. This is because when the seal is diving frequently (as during periods of shallow diving,

often associated with the near-shore zone) more transmissions will be received by the satellite (the seal is on the surface, and therefore transmitting more frequently). However, step 4 of the filtering process reduces the total number of locations by allocating a single location to each 6-hour bin (a maximum of 4 locations per day). By reducing the data to such few locations with each linked to a certain period of the day, this problem is largely overcome. Therefore, a positive feature of the filter is that it places a high weight on locations with a high level of confidence. Note however that if the process were to stop at step 3, as it does for location only instruments for which there are no behavioural data, then this problem would still exist and would need to be dealt with in some manner (see comments below).

I felt that this algorithm was well suited to the particular problems presented by SSL (i.e. frequent, short trips that don't move far from the haul-out site). The filter is a sophisticated development of other filtering approaches used by other groups in the field. The logic underlying the filter was basically sound, but the filter suffers from the same disadvantages of other versions in that it involved the progressive elimination of data, and quite severely reducing the number of locations that can be used in subsequent analyses. This "destructive" approach to data analysis has recently been replaced by new techniques that seek to maximise the data used, and to provide a maximum likelihood estimate of the path followed by seal, based on all the information available (see below).

The panel discussed the notion of conducting simulations to test the performance of the current algorithm in a similar way to that adopted by Thompson *et al* (2003) to assess their filter. This would involve developing simulated vectors of position with differing ARGOS location classes. Simulations of foraging trips could be built around time-line data from the SDRs. The empirical distributions of error determined for latitude and longitude already calculated by the SSL team could be used to introduce error into the simulated track. Application of the filtering algorithm to the modified path could then allow a formal comparison to be made between the true vector and the vector produced after filtering. It would also be possible to examine the performance of the filter using tracks with different degrees of location quality bias associated with different diving activities.

If these simulations show that the present filter is efficient at defining the movement patterns of seals in the context of their use of critical habitat, then the simplicity of the method means that it becomes an attractive option for the future. However, I suggest that whatever the outcome the SSL team should consider also using alternative techniques for other questions; this is because the scientific community considers alternative techniques as the way forward, and it is important for SSL team to be seen using the most up-to-date methods.

Alternatives to the NNML approach

There are some alternative approaches to filtering and smoothing tracks, as well as incorporating behavioural data into those tracks that NNML may choose to consider for future analyses.

Recently, a new approach to estimating animal tracks has been to use "path analysis" (Johansen *et al* 2003). A number of labs have been developing these techniques, such as the Myers turtle lab in Florida, the Sea Mammal Research Unit and my own lab at the University of Tasmania. Unfortunately, only the method developed by Jonsen *et al.* 2003 is published, but the other labs have the methods sufficiently developed to make them available to the SSL team if required.

The new path analysis models make use of maximum likelihood or Bayesian statistics and Markov chain analyses (Figure 1), and have several advantages over the more traditional filtering methods. Most importantly they make use of all the data. A second advantage is that, rather than producing a single “best path”, they can also produce a probability distribution enabling the incorporation of different levels of uncertainty due to location quality or frequency. This has the additional advantage of allowing one to interrogate the data at any regular temporal scale (“discretising” the data) overcoming problems associated with irregular timing of locations. Such discretised data offer a much more powerful mechanism for integrating behavioural and environmental covariates into subsequent analyses.

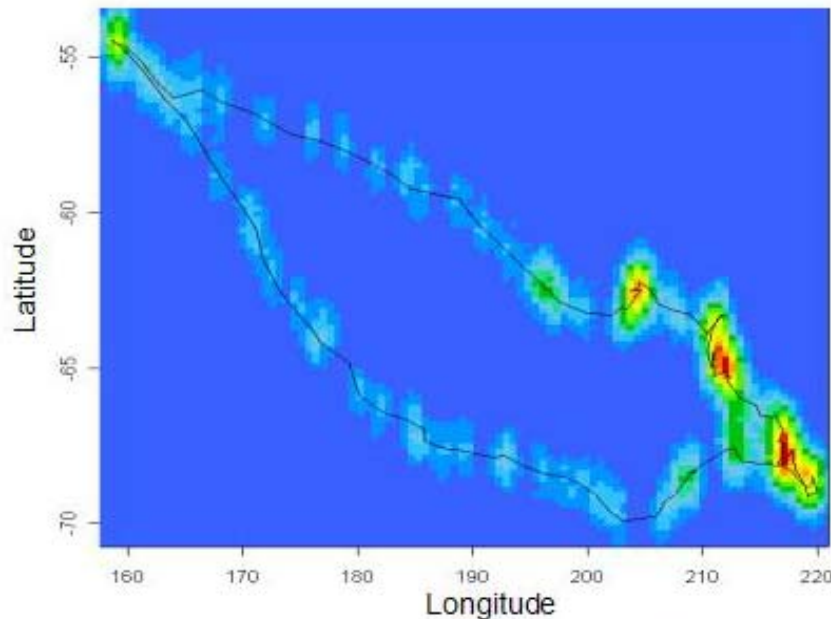


Figure 1: An example of a path analysis model from a satellite tracked southern elephant seal. The solid line is a conventional track, derived from a “destructive” filter. This is over-laid on a probability distribution, derived from Monte-Carlo Markov Chain analysis, incorporating swimming speed and location quality. Supplied by M.Sumner, Antarctic Wildlife Research Unit (unpublished data).

Unfortunately, implementation of the emerging techniques requires a high level of mathematical competence, usually beyond that of most biology graduates. I would suggest that at present the SSL team does not have the necessary mathematical skills, and needs a specialist to work alongside the biologists in Seattle to implement this and other types of high-level statistical approaches (such as the population level interpretations suggested in Section i).

Other analyses of the Telemetry data

One of the great strengths of the telemetry database compiled by the SLL team over the past two decades is the simultaneous collection of behavioural and location data made possible by the use of the SDRs. Despite the constraints imposed by the type of the units used to collect the data (see Section i), this is nonetheless a very important database, which contains information that is of considerable value. For example, the panel heard of the on-going analysis of the time-line (haul-out) data. Identifying trends in haul-out patterns of SSL are of vital importance in developing correction factors for both aerial and ground counts of seals, but have proven to be difficult to quantify using conventional techniques (observations or VHF telemetry). The time-line data have the potential to provide these key data, but more work is required to fully assess this potential. There are potential biases in the timelines that are received via satellites. Only 80% of time lines

are received, and it is possible that the remaining 20% relate to times that the seals are diving intensively (i.e. foraging), resulting in a biased sample (i.e. times not foraging) being transmitted.

There are also alternative approaches to analysing the behavioural data with respect to the seal's location at sea. The present filter reduced the data down to single location (admittedly of high quality) for each 6-hour period. An alternative approach (outlined in Appendix 1) is to use all the acceptable (post-filter) locations and to proportionally assign behavioural data to each location. This is a relatively simple approach (and does not need a specialist mathematician) and was developed to specifically address questions of behaviour relative habitat use.

Recommendations:

- The SLL team should perform simulations to test the performance of the NMML stage-based filter.
- The SSL team requires more mathematical support. The appointment of a mathematician based in Seattle to work developing the path analysis and spatial usage (state-space) analysis would ensure they continue as leaders in the field of marine mammal telemetry.
- Analysis of time line (haul-out) data should be continued, to give important supplementary information to population trends analysis.

iv. Determination of whether potential biases have been adequately identified, and whether appropriate measures of statistical uncertainty have been included

The panel discussed four sources of bias or uncertainty in the data from SDRs. These include:

- a. Instrument design and data collection protocols
- b. The representativeness of the sex and age classes in the population or the sample;
- c. The location of sampling;
- d. The type of analysis carried out on the data.

Discussion of several of these potential sources of bias have been covered the preceding sections but I will elaborate on the most pertinent sources below.

a. Instrument design and data collection protocols

The SSL team has recognised these biases and has, as far as possible given the types of SDRs being used, attempted to account for them in their collection and transmission protocols. The constraints of the existing SDR design and the ARGOS system require on-board summary of data before transmission, which means that some potential biases in the behavioural data (dive depth and timelines) may still exist. On-board summary strategies often incorporate some expectation of how the seals behave, for example the assumption that foraging only occurs on dives >4 m. This may result in underestimates to the extent to which foraging occurs. Other biases could arise because of gaps in the flow of information to the satellite due to the pattern of satellite coverage. If these gaps are caused by non-random distribution of behaviour it is likely that they will lead to biased estimates of behaviour. The solution to these issues is to move towards different SDRs that use different summary. New SDRs with more sophisticated data summary and transmission protocol MML should go a long way to helping to reduce this particular source of bias but it will not be completely eliminated.

The other issue to be aware of here is the quality of satellite locations. ARGOS assigns a quality to each of its estimated locations, based in part on the number of "hits" received by the satellite during its pass. If the seal is diving intensively while the satellite is overhead, it will spend less time on the surface, and therefore produce a lower quality location. By using path analysis methods (see Section iii) tracks can be expressed in terms of probabilities and the uncertainties accounted for. An important step in this process is to quantify the errors associated with different quality locations and the SSL team has already collected some of this information. However, it

may be important to quantify the uncertainty between individual instruments of the same design and between instruments of different design.

b. Representativeness by sex and age

Again, the SSL team has recognised this potential bias and has, over the years, moved to improve their capture techniques to eliminate them as much as possible, although it is still possible that the current catching methods contain biases. For example the SCUBA technique may catch more males than females, and offers only limited ability to select individuals. The technique is also likely to favour those juveniles that tend to spend more time near haul-out sites or those that are more likely to take bait because they are hungry. But it is important to stress that all biological studies include some degree of bias associated with sampling, and given the high level of difficulty associated with working with SSL, I feel the team has done a remarkable job. The implementation of the new catching methods (the raft traps) will enable the SSL team much greater control of the sex and age class of SSLs, but even these will have a level of bias associated with them.

The combined datasets of NMML and ADF&G consist currently of over 260 deployments. In line with the prevailing view that juvenile SSL are a key factor in the decline, most of these have been on young animals. Although this is undoubtedly one of the largest datasets for a marine mammal anywhere, when these data are stratified by region and time of year, sample sizes are considerably reduced. Nonetheless as outlined in Section ii there are sufficient numbers to attempt to assess the data in terms of the whole population of juvenile seals rather than in terms of samples.

c. Sample location

It is impractical to expect all possible SSL colonies to be sampled, but it is important that the sub-sampling of colonies is designed to reflect the range of characteristics (colony size, haul-out substrate, physical features of the inshore marine environment) demonstrated by the full range of colonies. If this is achieved, the information from the study colonies can be used in the "population level" models of spatial use to estimate usage pattern for the entire Aleutian chain. Again within the difficult logistic constraints the SSL team and the ADF&G have achieved good representative coverage of this region. Power analyses should however be considered to assess the level of individual variation in terms of the sample sizes at each colony.

d. Type of data analysis

Most of this has been covered in detail in section iii. Understanding the effects of bias and uncertainty requires the development of a model framework within which to investigate the sensitivity of the output to different levels of uncertainty and different types of bias. It would help NMML greatly in its interactions with fisheries managers, and in setting future research priorities, if it were able to use such a framework to illustrate these types of sensitivities.

Acknowledgements:

Along with the rest of the panel, I would like to thank the NMML Steller sea lion research team for the positive and helpful way in which it assisted with the review. Involved in the discussions were Dr Tom Loughlin, Jeremy Sterling, Bruce Robson, Kate Call, Michelle Lander, Angie Greg, Ralph Reem and Dr Tom Gilette (from the Alaska Department of Fish and Game).

References:

Hindell MA, Bradshaw CJA, Sumner MD, Michael KJ, Burton HR, 2003. Dispersal of female southern elephant seals and their prey consumption during the austral summer: relevance to management and oceanographic zones. *Journal of Applied Ecology* 40:703-715.

- Jonsen ID, Myers RA, Flemming JM. 2003. Meta-analysis of animal movement using state-space models. *Ecology* 84:3055.
- Matthiopoulos J, 2003a. Model-supervised kernel smoothing for the estimation of spatial usage. *Oikos* 102:367-377.
- Matthiopoulos J, 2003b. The use of space by animals as a function of accessibility and preference. *Ecological Modelling* 159:239-268.
- Matthiopoulos J, McConnell B, Duck C, Fedak M, 2004. Using satellite telemetry and aerial counts to estimate space use by grey seals around the British Isles. *J Appl Ecology* 41:476-491.
- Thompson, D., Moss, SEW., Lovell, P. 2003. Foraging behaviour of South American fur seals *Arctocephalus australis*: extracting fine scale foraging behaviour from satellite tracks. *Marine Ecology Progress Series*.

Appendix 1. Analysis of Wildlife Computers SDR binned behavioural data for crabeater seals (Extract from Wall, S. 200. The diving behaviour of crabeater seals, in relation to habitat characteristics in Eastern Antarctica. Honours thesis, University of Tasmania). A complete copy of the thesis can be provided if required.

Methods

SLTDR programming

The SLTDR tags (Wildlife Computers, Redmond, WA, USA) were programmed to collect and transmit data on several behavioural variables. These tags store summary information on maximum dive depths, dive durations and the amount of time spent at certain depths ("time-at-depth"). These data are encoded into a set of "bins" with user-defined limits (Table 3.1). Each bin contains counts for the number of dives in a give range of depths or time, accumulated over a period of six hours. Time-at-depth bins record a proportional count within each bin for each 6 hr period, thereby allowing the amount of time within each depth bin to be calculated Data are stored in this fashion for four reasons. 1. it reduces the amount of data storage that tags require and thereby reduces tag size and increases battery life. 2. By constraining data size it reduces the likelihood of satellites being overwhelmed with extraneous amounts of data 3. the time available for reception is limited by the overpass schedule of the satellites which precludes large amounts of data from being transmitted. 4. animal behaviour can influence transmission success because data can only be received by Argos if the antenna is out of the water long enough for a complete message to be transmitted.

The definition of the bins was revised following the first year of the study, making some aspects of the information on diving behaviour incompatible. This occurred because of an update in satellite tags and software in the later years. All tags recorded dive depths with a resolution of 2 m to a maximum depth of 500 m. The number of dives in each depth bin and the number of dives in each time or duration bin were recorded over all years, and the time spent diving in each depth bin was recorded from 1995 to 1999. The minimum depth to be considered a dive was set at 8 m during 1994 and 4 m between 1995 and 1999. This feature is important for two reasons: (1) it distinguishes between diving and surface swimming. (2) the rate that SLTDRs record information (10 second intervals) means a dive could be missed if it is not sufficiently long to bridge 10 seconds and be measured. The 1994 data were not included in the behavioural analysis due to the inconsistencies in the binned information between 1994 and 1995 to 1999.

Table 3.1. Maximum upper limits for each dive bin used to program satellite tags.

Year	Data	Upper bin limits
95 - 99	Dives per depth bin	10, 20, 30, 40, 50, 60, 70, 80, 90, 100, 150, 200, 250, >250 (metres)
	Dives per time bin	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, >13 (minutes)
	Time per depth bin	0, 4, 10, 20, 30, 40, 50, 60, 70, 80, 90, 100, 150, >150 (metres)
94	Dives per depth bin	20, 40, 80, 160, 320, >320 (metres)
	Dives per time bin	1, 2, 4, 8, 16, >16 (minutes)
	Time per depth bin	Not recorded

The amount of time spent hauled out was recorded as 0 m dives in the time per depth bin variable, and was only recorded after 10 consecutive dry transmissions. During 1994 the SLTDRs suspended measurements and transmissions after 15 hours "hauled-out", and resumed after the tag was "wet" for 4 successive at-sea transmission intervals. This preserved battery life and still allowed the total time hauled out to be calculated. Between 1995 and 1999 the tags remained active throughout haul-outs. Transmission intervals were approximately every 50 sec. at sea, and every 1:30 min when hauled out. Diving behaviour was recorded and stored in 6 hourly blocks (Table 3.2) for each 24 hr period, along with a date, time and geographical location.

Table 3.2. Six hourly time periods for each 24 hrs that SLTDRs bin information.

Period code	Time period (GMT)
0	13:00 – 18:59:59
1	19:00 – 00:59:59
2	01:00 – 06:59:59
3	07:00 – 12:59:59

Spatial data

Processing the behavioural data was achieved using a series of steps, and software outlined in Figure 3.1. As described in Chapter 2, Interactive Data Language (IDL 5.0 - Research Systems Inc., USA) was used to interpolate satellite location data to derive a 25 x 25 km grid over the study area, with filtered seal locations and crossing times for the entry and exit points for each grid cell along a each seal's track (Fig 3.1; Step 1). However, the existing routines did not calculate an exit point for the first grid cell or an entry point for the last grid cell of a seal's track, and the time spent in the first and last grid cells was lost. It was therefore necessary to manually view each seal's track in Arcview (Fig 3.1; Step 1.2) and extract the first location record and exit point for the first grid, and the entry point and final location in the last grid cell. As an example, (Map 3.1) I added an entry point and exit point for the first grid (Cell id 4131), by using the first location record as the entry point and using the entry point of the successive grid (Cell id 4132) as the exit point for the first grid. This was repeated for the last grid cell in the seals track, and was performed for all 23 seals to produce a set of corrected crossing time files.

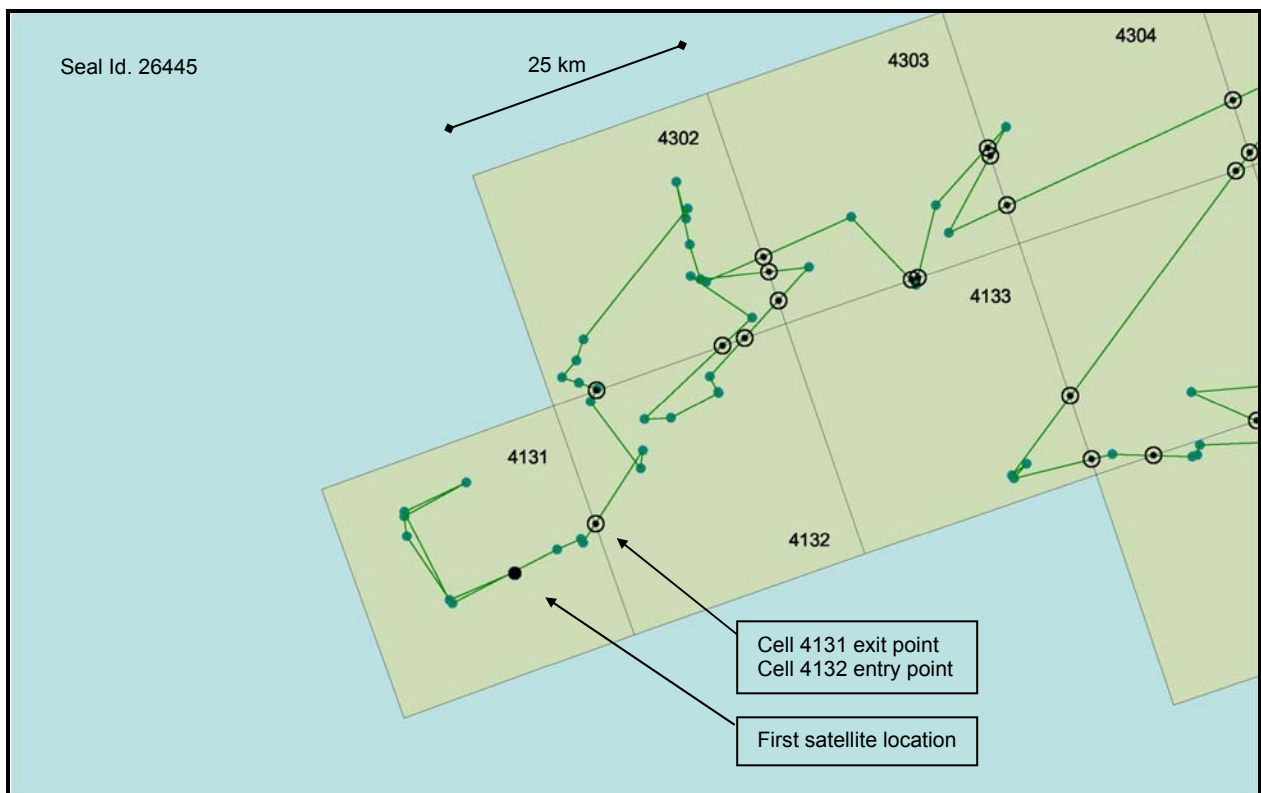


Figure 3.1. A portion of seal 26445's track showing the first few grid cells that it occupied. The track (green) is divided into segments between satellite location record, and the time and position it crosses a boundary between cells is interpolated in IDL.

I needed to partition the dive behaviours within each 6 hr block into the corresponding grid cell in order to investigate the relationships between diving behaviours and the physical environment. Because the SLTDRs summarised behavioural data in 6 hr bins, and stored them for 24 hrs before transmission, location data were uncoupled from behavioural data. All previous studies

using these types of tags have therefore not been able to put the behavioural data into a spatial context, making this the first study to geo-reference diving behaviours using SLTDR data in this fashion. I knew the geographic location of each grid cell, when a seal entered and exited grid cells, and the start and end time for each 6 hr block of diving behaviour. The task was to marry these three datasets to identify what diving behaviours occurred in what cells, and how they related to the environmental covariates.

This was achieved by writing customised macros in Excel (Step 2.1; App. #) to amalgamate the datasets. Each 6 hr block of diving behaviours (i.e. count data for behavioural histogram bins) was aligned chronologically with the grid cell crossing times of the particular seal, and assuming a constant rate of travel the proportional amount of each 6 hr time block was calculated for the corresponding grid cell. Using that time proportion, each diving parameter within a given 6 hr block was proportionately partitioned into that corresponding grid cell (Step 2.2; App. #). A simplified example is given in Figure 3.2. Binned diving data were condensed to a single variable using a weighted average across all bins.

Behavioural data could then be linked to the environmental data using grid cells as a cross reference (Step 3.1), which then enabled me to map the results and look at broad behavioural patterns graphically (Step 3.2). It further provided us with the critical link between location and behaviour which allowed me to explore the relationships between diving behaviours in crabeater seals and the physical environment.

A. Grid cell crossing times

Cell Id	Cell entry time	Cell exit time
2306	14/10/1997 11:40:00	14/10/1997 23:10:00



B. Dive depth data for period which coincide with grid cell no. 2306

Period	Start 6 hr block	End 6 hr block	4-10m	11-20m	21-30m
MD	14/10/1997 9:00:00	14/10/1997 15:00:00	20	12	5
AF	14/10/1997 15:00:00	14/10/1997 21:00:00	65	25	10
NT	14/10/1997 21:00:00	15/10/1997 3:00:00	120	150	80

C. Time and proportion of time in grid cell 2306

Hrs	%
3:20	56
6:00	100
2:10	36

D. Proportional allocation of dive count data to grid cell no. 2306

Cell Id	Period	Start 6 hr block	End 6 hr block	4-10m	11-20m	21-30m
2306	MD	14/10/1997 9:00:00	14/10/1997 15:00:00	11.2	6.72	2.8
2306	AF	14/10/1997 15:00:00	14/10/1997 21:00:00	65	25	10
2306	NT	14/10/1997 21:00:00	15/10/1997 3:00:00	43.2	54	28.8



E. A weighted average dive depth was used to determine the average dive depth per grid cell.

Cell Id	Period	Start 6 hr block	End 6 hr block	4-10m	11-20m	21-30m	Mean depth
---------	--------	------------------	----------------	-------	--------	--------	------------

2306	MD	14/10/1997 9:00:00	14/10/1997 15:00:00	11.2	6.72	2.8	12.3
2306	AF	14/10/1997 15:00:00	14/10/1997 21:00:00	65	25	10	11.0
2306	NT	14/10/1997 21:00:00	15/10/1997 3:00:00	43.2	54	28.8	14.9

Figure 3.2. Integration process for behavioural data. A. Grid cell crossing times produced by IDL. B. Dive depth data from satellite tags giving, the number of dives in a given depth bin, for a give 6 hr period. C. Proportional amount of a each 6 hr period in grid cell. D. Proportional number of dives for respective depth bins that occurred while the seal was in grid cell no. 2305. E. A weighted average was used to calculate the mean dive depth per grid cell. Bins were weighted by the centre of the depth range.

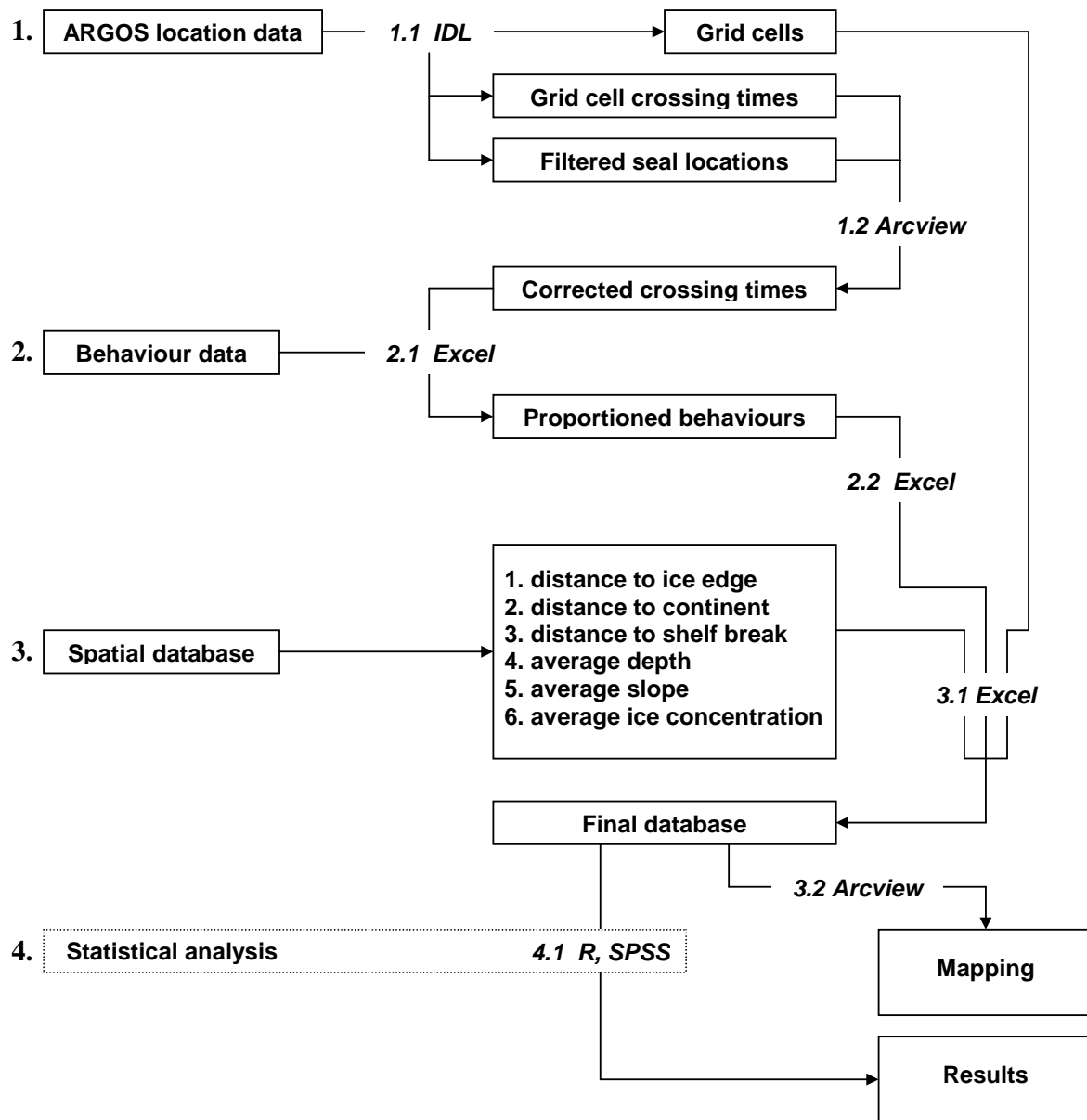


Figure 3.1. Data processing path for the behavioural dataset.

Statistical analyses

The behavioural dataset was temporally divided into a breeding and post-breeding season (Chapter 2). Unlike the spatial analysis, we were interested in broad and fine scale patterns in the behavioural data, therefore within each season the behavioural data were divided into broad spatial zones, and within each seasonal and geographical division I then examined the diurnal patterns in diving behaviours. We only used the two 6 hr daily blocks that corresponded with midnight and midday (NT = 21:00 - 3:00 and MD = 9:00 - 3:00, local time) for the diurnal pattern analysis.

Two behavioural parameters were analysed during the study; the number of dives per depth bin “dive depth” and the number of dives per time bin “dive duration”. A third dive parameter, the amount of time spent within each depth bin, was used to identify haul out periods.

To determine if behaviour varied between gender I examined the differences in the two response variables, ‘average depth’ and ‘average duration’ using a Student’s *t*-Test to test the mean response for each seal, grouped by gender. This was repeated for both the breeding and post-breeding seasons.

To determine if seasonal, geographical or diurnal patterns were influencing behaviour, a series of randomised chi-squared tests were applied to the frequencies of occurrences within each category [Roff, 1989 #17]. For large samples, a χ^2 contingency test is appropriate, however if the expected values within cells are very small, the calculated χ^2 may be inflated upward, and the use of the usual tabulated values of χ^2 to assess the significance of the observed value may be inappropriate. An alternate approach is to use Fisher’s exact permutation test, however the test suffers from the problem that the number of permutations of the data matrix increases factorially with the number of rows, columns, and total sample size [Roff, 1989 #17]. As a consequence, the number of required permutations increases astronomically with even modest increases in either the number of cells or sample size. To reduce the risk of too lower counts within categories the behavioural clumped into 5 categories (Table 3.3).

The approach taken here was to generate 1000 randomised 2 x 5 contingency tables subject to the constraint that column and row totals remain equal to those of the original data. If the expected distribution is designated by χ^2 , the observed value by χ_0^2 , and that for each randomized set by χ_r^2 . The estimated probability, *P*, of obtaining a value of χ^2 as large as or larger than that obtained from the actual observations χ_0^2 is given by $P = n/N$, where *n* is the number of randomizations that generate $\chi_r^2 \geq \chi_0^2$, and where *N* is the total number of randomised sets. Therefore if $\chi_r^2 \geq \chi_0^2$ occurs once in 1000 randomisations one can estimate the probability of this occurrence to be significant ($\chi_r^2 \geq \chi_0^2 = 1/1000$, i.e. $P = 0.001$). To be conservative in the interpretation of the results, we set our significance level for the randomised chi-squared to $P = 0.01$.

Table 3.3. Histogram bins for the randomised chi-squared tests. Values represent the upper levels of the bins.

Duration (min)	Depth (m)
3	10
4	20
5	30
10	50
> 10	> 50

Generalised linear modelling

I used the R statistical package (Ver. 1.7.1 (2003-06-16); <http://cran.r-project.org/>) to run Gamma GLMs with log link functions to model behavioural responses per grid cell as a function of the

physical environmental predictor variables (see Chapter 2 for details). A stepwise procedure based on the AIC was used to select the best fit model from the candidate models. I randomly sampled 50 % of the data for both the pre-breeding and breeding seasons, and use the remaining 50 % as a validation dataset. The significance of the best fit model terms was tested using analysis of deviance [McCullagh, 1989 #21].

High variance and differing distributions in the behavioural parameters did not enable strong models to be developed. Therefore, the approach taken was to generate a series of models using a backward stepwise selection routine starting from a saturated model with all the environmental parameters included. This was repeated 6 times for both behavioural parameters, and a best-fit model was constructed using environmental parameters based on the number of times a parameter as selected in the six candidate models, and by using analysis of deviance to establish parameter contribution. This was repeated for both the breeding and post-breeding seasons. GLMs were not developed for the two geographical zones individually as the seasonal models incorporate spatial components which would identify any geographical influences.

The predictive power of each model was assessed using a residuals plot to determine the deviance in the fitted values for the model, and a Quantile-quantile plot (QQ-plot), which determines if two data sets come from populations with a common distribution. The greater the departure from the 45° line, the greater the evidence that the two datasets have come from populations with different distributions.

Preliminary investigations of the data identified that the distributions of the behaviour responses were highly skewed to the left, were “short tailed” which makes fitting them to any exponential distribution family difficult. The dive depth data disproportionately biased the lower depth bin (4 - 10 m), therefore to try and discern deeper diving trends models were re-run with a minimum dive depth of 11 m.

APPENDIX II: Statement of Work

Consulting Agreement Between the University of Miami and Dr. Mark Hindell

May 21, 2004

Background

The NOAA Fisheries Alaska Fisheries Science Center (AFSC), National Marine Mammal Laboratory (NMML), requests a review of the analytical process used by AFSC scientists to delineate Steller sea lion dive and foraging behavior using satellite-linked dive recorders (SDRs). The data are used extensively by NOAA Fisheries to facilitate fisheries management in Alaska and to delineate critical habitat as required under the Endangered Species Act. The telemetry studies have been the focus of recent litigation, and were identified in court as a critical link in the Agency's decisions pertaining to Alaskan fisheries. It is important that Agency scientists use the best analytical methods available, and that their analysis be accepted by the peer community and Agency constituents.

A critical part of the analysis is the determination of the animal's location when foraging; the analysis leading to this determination requires data sorting and assumptions that can be viewed by constituents as equivocal. NMML developed a transmission protocol for SDRs to collect high-quality location data associated with six-hour sampling intervals. A stage-based filtering algorithm was also developed that used surface-timeline data to detect haul-out periods and iteratively evaluate the geometry and velocity of movements at sea relative to predefined threshold values. The filter also considered Argos location class of adjacent locations as a factor in determining which locations to remove. After filtering, locations were sub-sampled at 6, 12 and 24-hour intervals based on Argos location quality, and the effect of sampling design and filter algorithm was assessed using Schoener's ratio of spatial autocorrelation. The AFSC therefore requests an independent review of this analytical process.

General Requirements

The consultant will need to be thoroughly familiar with various remote sensing methods and basic computer programming and will travel to Seattle, WA, to meet with the involved scientists and to review the input data set and the analytical process. The AFSC will provide copies of relevant documents and a description of the analytical framework (see Appendix III).

The consultant shall review the Steller sea lion satellite telemetry data and the analytical procedures used to filter the data focusing on the following issues:

1. The appropriateness of the programming and deployment strategy of SDRs on juvenile Steller sea lions;

2. The appropriateness of the methods used to retrieve and manage telemetry data obtained from Service Argos;
3. The appropriateness of the stage-based filtering algorithm used by the NMML to detect haul-out periods and to evaluate the geometry and velocity of movements at sea; and
4. Determination of whether potential biases have been adequately identified, and whether appropriate measures of statistical uncertainty have been included.

The consultant shall be provided with background material (listed in Appendix III) to assist in addressing the aforementioned issues. NOAA Fisheries shall provide an agenda prior to the meeting at the AFSC.

The consultant shall conclude in a written statement whether the protocols and analyses represent the optimal approach and best analytical procedures for analyzing Steller sea lion satellite telemetry data for the purpose of managing affected Alaskan fisheries.

Specific

The consultant's duties shall not exceed a maximum total of 12 days - several days for document review, two days to attend a meeting at the AFSC, and several days to produce a written report of the findings. The consultant may perform most of the review, analysis, and writing duties out of the consultant's primary location, apart from the meeting, which shall be held at the AFSC. The written report is to be based on the consultant's findings, and no consensus report shall be accepted.

The itemized tasks of the consultant consist of the following:

1. Reading and considering the documents (listed in Appendix III) that provide context and background on the Steller sea lion telemetry issue.
2. Reading and analyzing the draft manuscript on the stage-based filtering algorithm and other documents describing NMML's telemetry data filtering protocol and data analysis.
3. Attending a two-day meeting in Seattle, Washington, from June 2-3, 2004, to discuss the review background material, the input data set, and the analytical process with AFSC scientists. The meeting will be held in Room 2039 of Building 4 of the Alaska Fisheries Science Center at Sand Point.
4. No later than June 18, 2004, submitting a written report¹ that addresses issues 1-4, as detailed in the above General Requirements section. See Annex I for additional details on the report outline. The report shall be sent to Dr. David Die, via email at ddie@rsmas.miami.edu, and to Mr. Manoj Shivilani, via email at mshivilani@rsmas.miami.edu.

¹ The written report will undergo an internal CIE review before it is considered final.

APPENDIX III: BACKGROUND MATERIAL ON STELLER SEA LION TELEMETRY STUDIES

Telemetry white paper prepared by NMFS and ADFG for the North Pacific Fisheries Management Councils Steller sea lion mitigation committee.

Addendum to the 2001 Endangered Species Act Section 7 Biological Opinion on the pollock, Pacific cod, and Atka mackerel fisheries off Alaska. Dated March 26, 2003.

Final Supplemental Environmental Impact Statement on Steller sea lion protection measures dated November 2001.

Fadely, B.S., B.W. Robson, J.T. Sterling, A. Grieg, and K.A. Call. In review. Immature Steller sea lion (*Eumetopias jubatus*) dive activity in relation to habitat features of the eastern and central Aleutian Islands. Fisheries Oceanography:

Merrick, R. L., T. R. Loughlin, G. A. Antonelis, and R. Hill. 1994. Use of satellite-linked telemetry to study Steller sea lion and northern fur seal foraging. Polar Research 13:105-114.

Merrick, R. L., and T. R. Loughlin. 1997. Foraging behavior of adult female and young-of-the-year Steller sea lions (*Eumetopias jubatus*) in Alaskan waters. Canadian Journal of Zoology 75 (5):776-786.

Loughlin, T. R., A. S. Perlov, J. D. Baker, S. A. Blokhin, and A. G. Makhnyr. 1998. Diving behavior of adult female Steller sea lions in the Kuril Islands, Russia. Biosphere Conservation 1 (1):21-31.

Loughlin, T.R., J.T. Sterling, R.L. Merrick, J.L. Sease, and A.E. York. 2003. Diving behavior of immature Steller sea lions (*Eumetopias jubatus*). Fishery Bulletin 101 (3):566-582.

Robson, B.W., M.E. Goebel, J.D. Baker, R.R. Ream, T.R. Loughlin, R.C. Francis, G.A. Antonelis, and D.P. Costa. 2004. Separation of foraging habitat among breeding sites of a colonial marine predator, the northern fur seal (*Callorhinus ursinus*). Canadian Journal of Zoology 82 (1):20-29.

Robson, B.W., A. Greig, J.T. Sterling, and B.S. Fadely. Draft ms. Use of an integrated approach to programming and filtering data from satellite-linked dive recorders: applications for habitat conservation of endangered Steller sea lions.